10

Aspects of Social Behavior in Fiddler Crabs, with Special Reference to *Uca maracoani* (Latreille)[1,2]

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(Plate I; Text-figures 1-5)

[This paper is one of a series emanating from the tropical Field Station of the New York Zoological Society at Simla, Arima Valley, Trinidad, British West Indies. The Station was founded in 1950 by the Zoological Society's Department of Tropical Research, under the direction of Dr. William Beebe. It comprises 200 acres in the middle of the Northern Range, which includes large stretches of undisturbed government forest reserves. The laboratory of the Station is intended for research in tropical ecology and in animal behavior. The altitude of the research area is 500 to 1,800 feet, with an annual rainfall of more than 100 inches.

[For further ecological details of meteorology and biotic zones see "Introduction to the Ecology of the Arima Valley, Trinidad, B. W. I.," William Beebe. (Zoologica, 1952, Vol. 37, No. 13, pp. 157-184.)]

CONTENTS

I. INTRODUCTION

THIS paper is a preliminary report on recent studies of social behavior in tropical fiddler crabs, conducted both in the field and in captivity. It is concerned with activity rhythms determined principally by light and tide, with changing phases of behavior under internal control, and with expressions of agonistic and epigamic behavior. All of these topics will be more fully developed in a monograph on the genus *Uca,* now in preparation.

A general account of the field work undertaken in the present study has been given in a recent paper (Crane, 1957), in which it is stated that observations and motion picture records on the behavior of many species were made in Southeast Asia, the South Pacific and the neotropics. Since then a summer has been spent on the east and west coasts of Africa.

Throughout the previous seasons of the work the need for supplementary observations on captive crabs was felt with increasing force. Because so much territory had to be covered, stays in one locality of more than a week were infrequent. More leisurely study periods, ranging from ten days to two months in length, were accomplished in Panama, Tahiti, Fiji, Singapore, Zanzibar and Angola, but even during these periods certain observations were necessarily meager. Everywhere the deficiencies were felt particularly in data concerning behavior sequences in individual crabs and in those concerning territoriality.

Accordingly, during the winter and spring of 1958 a group of four local species of *Uca* was established in captivity in Trinidad. The species selected were *maracoani, thayeri, rapax* and *cumulanta* (Table I). All four live sympatrically on mudflats that are surrounded by mangroves and adjacent to the open waters of the Gulf of Paria. The locality, known as Cocorite Swamp, lies in the suburbs of Port-of-Spain.

The data reported in the present paper are altogether observational. Experimental studies, paralleling those of Brown and his co-workers (1954, and refs.) on the diurnal, tidal and semi-

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TABLE 1. SPECIES, AUTHORITIES, REFERENCES AND RANGES OF *Uca* MENTIONED IN THIS CONTRIBUTION

Species	Taxonomic Reference and Comment	Range
annulipes (Latreille)	Barnard, 1950, p. 97	East Africa to Philippines
chlorophthalmus (Milne-Edwards)	The African form, as characterized by Barnard, 1950, p. 95	East Africa
cumulanta Crane	Crane, 1943, p. 42	Tropical Western Atlantic
latimanus (Rathbun)	Rathbun, 1918, p. 422	Tropical Eastern Pacific
maracoani (Latreille)	Rathbun, 1918, p. 378	Tropical Western Atlantic
marionis (Desmarest)	Barnard, 1950, p. 90	East Africa to Samoa
pugilator (Bosc)	Rathbun, 1918, p. 400	Eastern & Southern United States
pugnax (Smith)	Rathbun, 1918, p. 395	Eastern United States south to Northern Florida
rapax (Smith)	Tashian, 1958, p. 89 Syn.: *pugnax rapax* Rathbun, 1900, p. 7; 1918, p. 397	Western Atlantic: North Florida to Brazil
stenodactylus (Milne-Edwards & Lucas)	Rathbun, 1918, p. 416	Tropical Eastern Pacific
thayeri Rathbun	Rathbun, 1918, p. 406	Western Atlantic: North Florida to Brazil
urvillei (Milne-Edwards)	The African form, as characterized by Barnard, 1950, p. 93	East Africa

lunar influences on chromatophore expansion and oxygen consumption, have not yet been undertaken.

Particular thanks are due to my co-workers, Dr. William Beebe, Mr. Henry Fleming and Dr. D. W. Snow, as well as to Mr. M. Woodbridge Williams of the National Geographic Society, for advice and cooperation in the inauguration and operation of the outdoor terrarium at the Trinidad Field Station of the New York Zoological Society.

II. MATERIAL AND METHODS
(Plate I)

The method of maintaining the crabs far from the sea at the laboratory's altitude of 800 feet proved to be surprisingly simple. A cement-lined lily pond, measuring 5½ by 14 feet in area and 16 inches in depth, was emptied of all plants and drained. Tubfuls of mud from the crabs' native swamp were heaped across one end of the pool which, in one corner, was adjacent to a small, fresh-water marsh. The latter, established for the original lily pond, was maintained for the crab terrarium in order better to conserve moisture in the marine mud during the dry weather. The mud was fashioned into a gently sloping bank measuring about 40 square feet in area and having a maximum depth of 11 inches. Narrow strips of window glass were thrust into the mud against the cement walls of the pool, framing it on three sides to provide a surface which could not be scaled by the crabs. Since the fiddlers, once they had settled in, never wandered along the bottom more than a few inches, it was unnecessary to line the sides completely.

A "tide" was found to be essential in order to induce a level and variety of social activity adequate for the work. However, an exceedingly rough approximation of natural tidal conditions proved adequate for the present purpose. Briefly, it was sufficient merely to fill and empty the pond with a garden hose on an approximately 25-hour schedule that resembled the daylight tidal schedule in Cocorite, the local swamp.

In practice the system worked as follows: The artificial mudbank was always completely exposed at the hour of local daylight low tide, as well as, variously and irregularly, for one to three hours both before and after that time. No attempt was made to drain or fill the pool in accordance with the natural tidal rate, since this factor was found not to affect noticeably the crabs' activities. Filling of the pool required between two and one-half and three hours and drainage about forty minutes.

In the first two weeks of the work spring and neap tides were roughly simulated on the appropriate dates, but this too proved to be a refinement unnecessary for the present study. Although the height of high tide was made slightly and irregularly to vary, a small area at the top of the bank was always left exposed.

After the first few days no attempt was made to shift the tides twice daily; only the daytime low tide was represented. Every two weeks, however, as low tide coincided roughly with dawn and dusk, the water level was either kept low for some eighteen hours (as from 3 P.M. to 9 A.M.), or else two natural 12-hour-plus tides were provided for that particular 25-hour period; this arrangement made the shift from a late afternoon to an early morning "low." No attempt was made to make the shift at a particular corresponding tide fortnightly; it was simply done as convenient when the local tide occurred between five and eight o'clock. This shift was purposely made differently, at different hours, from fortnight to fortnight, to avoid establishing any artificial rhythms; no trace of such a result was evident, and the behavior of the captive crabs remained in harmony with that of the source populations in the mangrove swamp. Field trips were made to that area for comparative observation at frequent intervals throughout the four and one-half months of the observations.

Fresh water piped from mountain springs, used for all purposes at the Station, was provided for the pool. A sample, as tested by the Government Chemist's Department of Trinidad, contained 0.288 parts per thousand of dissolved salts. This was in contrast to 34.5 parts per thousand of dissolved salts at high tide, during the dry season, of the Gulf of Paria at the point where the water was flooding into Cocorite Swamp. At the height of the rainy season water from crab holes and an adjacent ditch, at low tide, proved almost as salty—33.7 and 33.8 parts per thousand, respectively. Swamp water tested earlier (Crane, 1943) in a Venezuelan habitat of the same species gave much lower salinities, ranging from about 5 to 7 parts per thousand during the rainy season. None of these species, however, was ever found in fresh water.

Their ready adaptation to tap-water tides in the crabbery was explained when water from these burrows was analyzed. Although the mud had been unchanged for several weeks before each analysis, and was subjected to gentle flooding daily, samples taken in March, April, May and June contained respectively 7.73, 8.36, 13.2 and 8.15 parts per thousand of dissolved salts. All these figures, judging by the previous Venezuelan analyses, are within the normal toleration of the species. Since only pure mud from the native swamp was used in the crabbery, it was originally strongly impregnated with salts and held them well; the drainage was in fact so poor that water remained standing in the lower parts of the burrows even on hot and dry days when the pool had been otherwise drained for an entire tidal period.

In spite of this poor drainage, the mud never gave off any odor of decay. Most of the few crabs that died did so on top of the flat. No food material was ever added to the mud, and the crabs fed normally by sifting organic matter from it. Aside from the daily draining and filling of the pool, the only maintenance performed was the addition, once every three or four weeks, of a fresh layer of mud from Cocorite Swamp. Although the material was always spread very roughly over the existing bank, which had become lowered by erosion, within a day the crabs and the changing water levels removed all traces of disturbance.

Marine toads (*Bufo marinus*) proved to be the only nuisance, since they came in crowds to the pool at night. The extreme top of the bank was always exposed, and they did minor damage by knocking over burrow markers, leaving slime and eggs and, probably, eating occasional small crabs whose disappearance was otherwise unexplained. A foot-high fence of copper netting, soon erected, kept the toads out.

Garden plant flags, made of magnesium and marked with waterproof ink, identified burrows for territorial studies. Individual crabs were painted for recognition with spots of quick-drying lacquer in various colors and positions. Marks on the anterior part of the carapace and outer edge of the major cheliped were best for both visibility and durability. Providing the paint was not applied to pilous or tuberculous areas, the marks remained distinct for about a month.

Observations were conducted principally from an eight-foot-high platform standing near the pool. A 20-power monocular enabled even minor mouthpart motions to be seen. From this position the crabs were undisturbed by the observer's movements, and the entire mudbank could be easily overlooked.

It was found that the optimum population level was not more than about 5 to 7 males and a similar number of females of *U. maracoani*, the largest species. A total of 35 crabs of all species was never exceeded at any one time.

The success of the terrarium for these species is attested by the following facts: two *maracoani* survived healthily the entire period of observation, which comprised more than four and one-half months; fifteen of three species were kept between one and three months. The only losses were as follows: senility or disease (six), accidental poisoning by the addition of unseasoned lime blocks, escape of small crabs up the glass which had been coated with mud by splashing during heavy rains and, apparently, predation by marine toads. Other specimens were killed after various periods for drawing and dissection. All species displayed and courted, all except *cumulanta* were seen to mate from one to four times; several immature *maracoani* females molted to the adult stage; and, finally, at least five *thayeri* females and one *maracoani* laid eggs.

Throughout the study the behavior of the original populations in Cocorite Swamp was checked at least once every ten days for comparison with the activity level in the terrarium.

Henceforth the term "crabbery" will be used for the converted lily pond described above.

III. Tidal and Semilunar Rhythms in Activity

The activity levels of fiddler crabs are influenced by the following major factors of the external environment: light, tide, temperature, surface moisture and rain. The general conditions for high activity in populations are known to any observer who has repeatedly watched these crustaceans. As a whole the crabs are most active during several hours before and after low tide on warm, sunny days; the optimum time of day, other factors being favorable, is often the midmorning. As with many intertidal animals, spring tides are especially favorable to species living close to either low- or high-tide levels. With one or two exceptions the crabs are diurnal. Conversely, adverse conditions include darkness, submersion of the habitat by the tide, temperatures unfavorable to the species, extreme drying of the habitat and heavy showers. If one external factor becomes strongly unfavorable, all activity in a population is suppressed, the crabs retiring underground and remaining there for any required period, from minutes to a season, until conditions improve.

Laboratory investigations have shown that some of the chromatophores in *Uca pugnax* and *pugilator* expand in accordance with at least two of the aforementioned external factors favorable to activity—daylight and the hours of low tide. Under ordinary conditions, these *Uca* are typically darker by day and paler by night, showing a distinct 24-hour rhythm (Welsh, 1938; Brown & Webb, 1948; Webb, 1950; Brown & Stephens, 1951; Brown & Hines, 1952). Superimposed on this daily rhythm is a tidal rhythm which effects a secondary daily expansion of the chromatophores at the time of low tide. In normal tidal cycles, therefore, this secondary expansion occurs on the average some forty-nine minutes later every day. Accordingly the two superimposed chromatophoric schedules come into synchrony every fortnight, resulting in a semilunar rhythm (Brown, Fingerman, Sandeen & Webb, 1953; Brown, 1954; Brown, Webb, Bennett & Sandeen, 1954; Fingerman, 1956). The rate of oxygen consumption shows similar diurnal and tidal rhythms (Brown, Bennett & Webb, 1953). The various rhythms have been shown to persist in the laboratory over considerable periods, and are independent of a wide range of temperatures. They appear to be established originally by local conditions of light and tide, probably early in the life of the young crab.

Recent studies reveal additional complexities. Fingerman (1957) found that the tidal rhythm in *pugilator* varies with the height of the burrows above low water; chromatophores in crabs from the higher levels expand earlier, apparently in accordance with their earlier uncovering by the tide.

Tidal Rhythms.— The work in the Trinidad crabbery showed that behavior in fiddlers, and particularly their social behavior, is also influenced by light and tide. If the induced daytime tide did not correspond roughly with the natural hours of ebbing and flowing at Cocorite, the native habitat of the captive crabs, feeding activity was much reduced and social behavior almost or wholly absent. If the water level in the crabbery was kept constant, at any level, evidence of the crabs' original activity rhythm was clearly apparent: although activity was far below normal, the crabs emerged from their burrows, fed and, for several days, waved and fought almost entirely during the normal periods of maximum activity at Cocorite.

In spite of the unnatural and irregular 25-hour rhythm under which the crabs were eventually maintained for more than four months, and the abnormal rapidity of the raising and lowering of the tides, traces of this natural rhythm were shown by the oldest inhabitants of the crabbery to the end of the period of observation.

Since the purpose of the crabbery was merely to supplement field observations on social behavior, no attempt was made to condition the crabs to a different tidal rhythm. It is hoped that this preliminary study will lead to experimental inquiries conducted under appropriately controlled conditions.

Semilunar Rhythms.— A related result of the crabbery work was the observation that a semilunar rhythm also exists in the social behavior of *Uca* and is also governed by a time-clock that is largely independent of external conditions. The factors responsible for this rhythm seem unquestionably to be a particular combination of time of day with time of low tide. That is, there is evidence of a fortnightly rhythm in social behavior corresponding to that found in the behavior of the crabs' chromatophores. It appears also to be similar to some of the semilunar rhythms concerned in the breeding and other behavior of numerous marine animals (Korringa, 1947, and refs.).

Field observations in the Indo-Pacific area during the past several years suggested that the highest levels of social activity in fiddler crabs, particularly in more primitive species, appear fortnightly and that the periods of maximum activity occur at different times of the day, depending on the species. In general the primitive crabs become active earlier in the morning than more advanced forms, and hence would be optimally suited by an earlier hour by low tide.

As a notable example three species may be cited which live contiguously on the Island of Pemba, East Africa. The primitive narrow-front, *urvillei*, reached the height of its display period by 8:30 A.M. and its waving practically ceased by 10 A.M., regardless of the favorableness of the tide. In contrast the moderately advanced species, *annulipes*, although its burrows, being higher on the shore, were uncovered earlier than those of *urvillei*, did not display fully until around 10 o'clock. Display then continued even during the heat of the day, at temperatures which often temporarily inhibit waving in other species, and stopped only in the late afternoon when the tide was lapping at the burrows. The third species, *chlorophthalmus*, fell between the other two in hours of waving; its phylogenetic position also appears intermediate between those of *urvillei* and *annulipes*.

Obviously the waving period of the primitive *urvillei* was limited to a low-tide hour falling between 6 and 9 A.M., since it lived on mudflats exposed less than four hours daily, and since, like other fiddlers, it did not become fully active before about 7 A.M. Whether its midday activities were curtailed by light intensity or temperature or both, or by some other factor, is unknown; also, unfortunately, my stay was not long enough to observe its behavior when low tide occurred during the late afternoon.

In Trinidad the four species under special observation were found to have similar differences of maximum activity in respect to tide and time of day (Table 2). The most primitive of the crabs, *U. thayeri*, was most active socially when low tide in its native swamp was reached between 6 and 9, field observations being made as appropriate in either the late afternoon or early morning. In previous years, before it was known either that this crab is primitive and so displays relatively little, or that its diurnal pattern is distinct, I had rarely and incompletely observed its display and had formed erroneous ideas of its display season.

The other three species observed at Cocorite Swamp and in the crabbery showed similar distinctions in maximum display activity. Optimum low tides for *maracoani* were found to occur between 8 and 10 A.M., while for *rapax* and *cumulanta* the corresponding times are somewhat later, approximately between 8 A.M. and noon, although the evidence is not so complete.

Tides occurring between noon and 5 P.M. are disadvantageous to all four Trinidad species, and to the majority observed in other parts of the world. The few exceptions seem to be confined to the highly developed species, particularly in the Pacific neotropics. For example, when physiological conditions, weather and tides are all favorable, *stenodactylus* and *latimanus* display strongly at any time of the day from midmorning to near sunset, with only brief respites during exceptionally hot midday periods.

Enough has been said to show that various species are most active socially at various combinations of light, tide and, almost certainly, temperature. The activity is not purely a prompt response to external conditions, however, since crabs both at Cocorite Swamp and in the crabbery behaved in accordance with favorable and unfavorable periods of the fortnight regardless of light and temperature. On cool afternoons at low tide, the crabs showed no notable increase in waving behavior, nor did cloudy (but not densely overcast) mornings decrease the amount of waving during their optimum hours of activity. Similarly, on brilliantly sunny days the crabbery remained mostly in the shade, being only intermittently and briefly dappled with sun, until 1:30 P.M., while the surface temperature stayed virtually unchanged between 9 and 1:30. This temperature, ranging between the mid-seventies and the low eighties (approximately 24°-29° C.) is the optimum for waving activity in *thayeri* and *maracoani*. Yet, except for rare individuals of exceptionally low threshold, waving in both species virtually ceased when low tide fell after 11 A.M. Repeated observations at Cocorite, on relative degrees of waving under various conditions, corroborated the observations made on the miniature population in the crabbery.

IV. Phases of Behavior under Internal Control

A rough diurnal sequence of activities is usually apparent in any population of *Uca*. Feeding, display and, again, feeding combined with burrow repairs typically follow in sequence as the dominant activity during any low-tide period (Crane, 1941; Altevogt, 1955.2, 1957).

Table 2. Indications of Semilunar Rhythms in the Display of *Uca* spp. in Captivity

Moon	Date	Tide (Day Low)	Display	Moon	Date	Tide (Day Low)	Display	Moon	Date	Tide (Day Low)	Display
Last Quarter	Feb. 10	15:58	— — —	Last Quarter	Mar. 12	16:39	— — —	Last Quarter	Apr. 10	16:11	— — —
	11	17:17	— — —		13	18:24	M — —		11	17:38	m — —
	12	18:45	— — —		14	7:00	— — —		12	6:34	m — —
	13	6:58	— — —		15	8:13	M T R		13	7:48	M t —
	14	8:08	M — —		16	8:51	M T R		14	8:26	M t —
	15	8:53	M — —		17	9:15	M T R		15	8:49	M t —
	16	9:23	M t —		18	9:31	m t —		16	9:07	M t —
	17	9:46	?		19	9:49	m t —		17	9:28	M — R
New	18	10:07	M — r	New	20	10:12	m t R		18	9:54	M t r
	19	10:30	— — r		21	10:41	m T R	New	19	10:25	M t R
	20	11:00	— — r		22	11:16	m — r		20	11:01	M — R
	21	11:35	m t R		23	11:54	— — r		21	11:40	— — R
	22	12:14	— T r		24	12:36	m t r		22	12:24	m — —
	23	12:58	m t r		25	13:22	m — —		23	13:08	— — —
	24	13:45	— — r		26	14:14	— — —		24	13:58	m t —
	25	14:42	m — —		27	15:18	— — —		25	14:55	— — —
First Quarter	26	15:51	?	First Quarter	28	16:42	— — r	First Quarter	26	16:04	— t —
	27	17:12	?		29	18:10	— T r		27	17:25	— — —
	28	18:23	— — —		30	6:28	— T —		28	6:08	m — —
	Mar. 1	6:48	— T —		31	7:33	M T R		29	7:11	m — —
	2	7:50	— T —		Apr. 1	8:21	M T R		30	8:02	— — —
	3	8:39	— T —		2	9:04	M T R		May 1	8:46	m t —
	4	9:23	m T —		3	9:47	M T R		2	9:29	— — R
Full	5	10:07	?	Full	4	10:31	M t r	Full	3	10:13	m — r
	6	10:52	— — r		5	11:18	m t r		4	10:58	M — R
	7	11:40	— — R		6	12:07	m — R		5	11:45	m — R
	8	12:31	— — r		7	12:58	m t r		6	12:34	— — R
	9	13:25	— — r		8	13:55	m — —		7	13:26	M — R
	10	14:23	— — —		9	14:56	— — —		8	14:19	M — R
	11	15:29	— — r						9	15:17	M — R

Key

m: Display, usually infrequent and of low intensity, by minority of *maracoani.*
t: Display, usually infrequent and of low intensity, by minority of *thayeri.*
r: Display, usually infrequent and of low intensity, by minority of *rapax.*
M: High display activity by half or more *maracoani.*
T: High display activity by half or more *thayeri.*
R: High display activity by half or more *rapax.*
—: No display in *maracoani* when bar is on left,
thayeri when bar is in center,
rapax when bar is on right.
?: Observations inadequate.

Note

From five to nine adult males of each species formed the daily basis of the data. Because of the number of variables a numerical analysis of this material seems unwarranted. Nevertheless, inspection of the table clearly shows a preponderance of display activity on dates when low tide occurred during the morning hours. The atypical pattern in May was probably the result of five days of high rainfall that began on April 28 and marked the end of the dry season. Data on the display of the fourth species, *U. cumulanta,* were insufficient for inclusion.

When the behavior of individual crabs is observed, however, wide variations are shown in the amount of time spent in feeding, fighting, wandering about and display. Many do not display at all, some remain almost inactive, others feed more than usual and a few wander through the population repeatedly dispossessing other males of their burrows and then passing on. Observation of the same individuals over successive days shows that there is often an overnight shift in the dominant type of activity. The first evidence of these shifting phases was obtained in Panama (Crane, 1941, pp. 160, 196). Similar observations (unpubl.) have since been made on a number of additional species in both hemispheres.

Attempts to keep track of individuals in the field by marking them with paint were made in Panama, Singapore and Zanzibar. Little success was attained; the great majority of the crabs were not seen again after two or three days. Another difficulty was the limited study time available for any one locality. Altevogt, on the other hand, working principally with *annulipes* and *marionis* in India (1955.2, 1957), secured good results in measuring the distances traveled by marked *marionis* between successive low tides. He was also able to keep track of certain individuals well enough to determine that they usually retained their paint for two to three weeks. Although these specimens showed the usual daily sequence of activities, with wandering or waving-and-fighting sometimes accentuated, sequential phases in the present sense were apparently not noticeable in either of his species.

Phase Characteristics.— One of the principal reasons for establishing the Trinidad crabbery was to keep individuals under close observation for long periods. In each of the four species maintained in the crabbery, five or six distinct phases were apparent. Although data were accumulated on individuals in each species, close and continuous daily observations were confined to adult male *U. maracoani* (Text-fig. 1). In this species the phases and their characteristics are as follows:

1. *Underground Phase.* The crab does not emerge from the burrow during at least one entire period of low tide.

2. *Phase of Maintenance Activity.* Activity is confined to feeding and repair of original burrow. Aggressive or defensive behavior is lacking, the crab always giving way to an intruder without threat postures or fighting (Text-figs. 2, 3); no apparent attention directed toward females; no display.

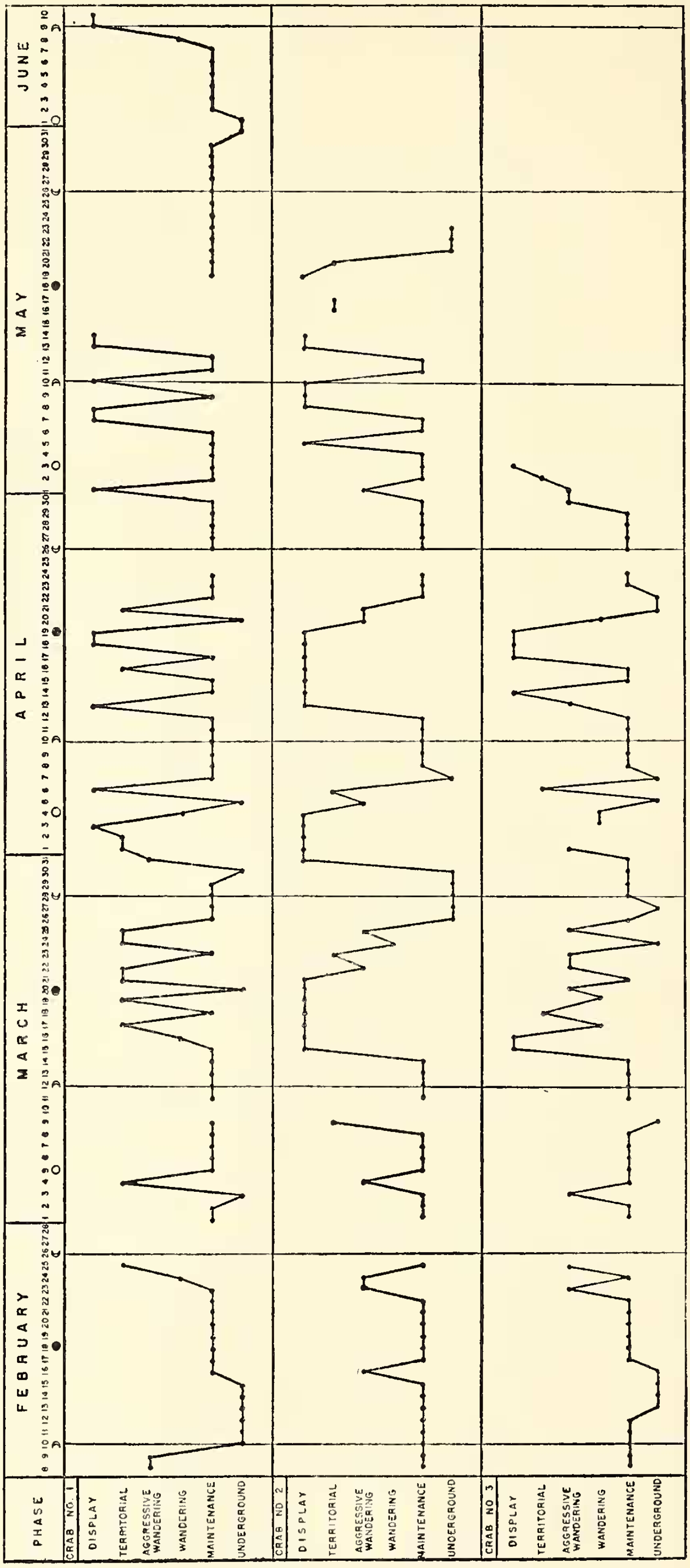
3. *Non-aggressive Wandering Phase.* At its peak this phase is characterized by almost ceaseless walking during low-tide periods, punctuated by periods of feeding. Feeding is often near the water's edge, rather than in the vicinity of burrows. In the crabbery no fixed route is followed, although it is often roughly circular, embracing the entire circumference of the mudbank and obviously limited by the barriers. When in the vicinity of the walls, the crab often attempts to climb the glass repeatedly, clawing at the smooth surface for minutes at a time. Only crabs in this phase and the one following ever show this behavior. As in Phase 2, defensive, aggressive and display behavior, as well as overt responses to females, are altogether lacking.

4. *Aggressive Wandering Phase.* In this phase the crab covers almost as much territory as in the preceding, but the wanderings are punctuated with attacks on burrow-holding males. These attacks may or may not be successful: the tenant, if he is in one of the foregoing, non-aggressive phases, usually abandons the burrow and goes promptly away, although he may hold out for a while by retiring underground. In encounters between males in any of the higher phases the result is uncertain. Typical of this phase is the abandonment of the newly-won burrow by the aggressor, usually very soon after the departure of the former tenant. Pursuit of females, followed by covering and ritualized feeding from their carapaces (p. 127 and Text-fig. 4), begins in this phase, although mating does not take place.

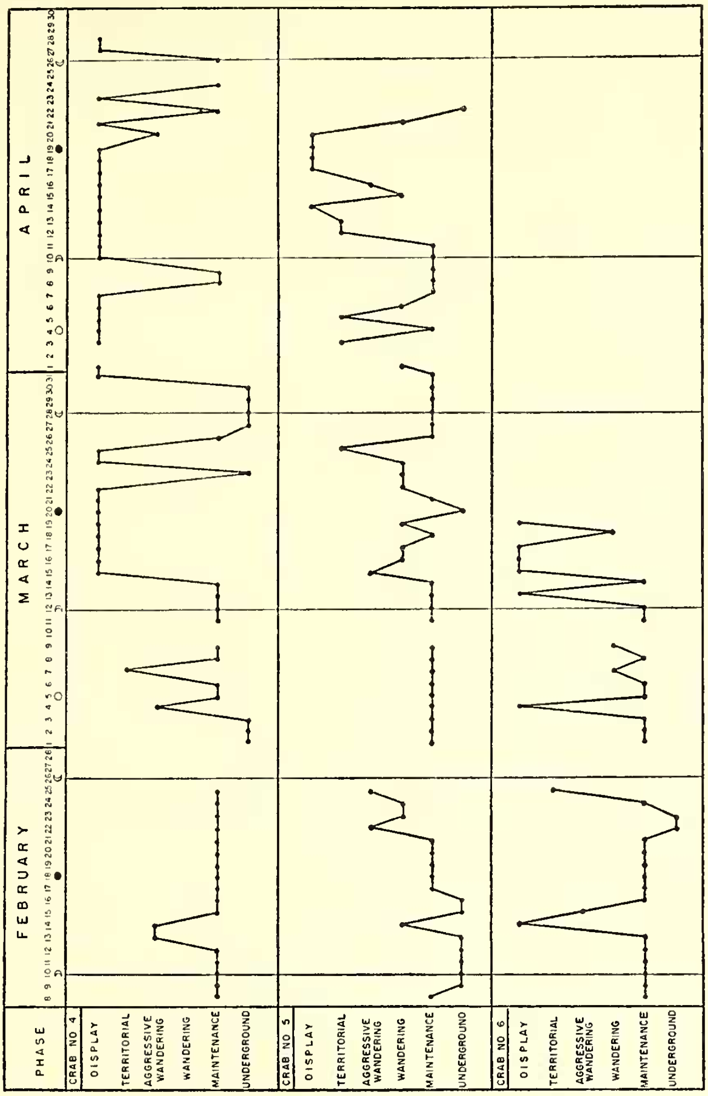
5. *Territorial Phase.* In this phase, usually brief, a crab takes possession of a burrow and attempts, often successfully, to ward off aggressors with threat and fighting. Preliminary courtship, as in the preceding phase, occurs without display.

6. *Display Phase.* A crab that displays during any time of a given day is considered to be in the display phase. Complete courtship, including copulation, is confined to individuals that display at some time of the same day, although waving does not always in this species immediately precede mating in surface courtships, and there is no display except in the immediate vicinity of a burrow held by the displaying crab. As in many species observed in the field, the burrows of displaying crabs are usually on the higher part of the bank. Such a burrow, which may be held by the same individual for a number of days during the display phase, is often the same one taken over by the crab during its territorial phase.

Sequence Characteristics.— To a certain extent these phases are recapitulated each day and during every semilunar period. Even crabs at



TEXT-FIG. 1 (part). See caption below.



TEXT-FIG. 1. Phase sequences in the behavior of six adult male *Uca maracoani* in captivity. The position of each dot indicates the highest type of activity attained by an individual on a particular date, when these types are arranged in a series from least social to most social. The complete natural sequence appears to range from uninterrupted inactivity underground, through simple maintenance (feeding and digging) activities, wandering, aggressive wandering, territoriality and, finally, display. See text, p. 117 ff.

Gaps in the diagrams represent days when observations were missing or inadequate. The graph of each individual's activity ends with the day before its death.

These specimens were selected for illustration because of their longevity. The shorter records of fifteen other individuals showed similar characteristics.

the height of a display phase feed briefly, often away from the burrow near the water, and all crabs spend inclement periods underground.

Ideally the phases may be traced, in sequence, over a period of days or weeks in individual crabs. In practice, however, one or more phases are frequently omitted, curtailed or superimposed on the preceding. The territorial phase is very often curtailed, emerging abruptly from the end of the aggressive wandering phase and almost at once giving way, on the same day, to a display phase. These changes on single days are not indicated in Text-figure 1, which shows only the highest type of activity attained by an individual on a particular date, when these types are arranged in the series described above from least to most social.

At the end of a display phase the sequence is rarely reversed. Rather, the crab frequently subsides abruptly into a maintenance phase, which may or may not deteriorate further into a period passed underground.

It will be noted that in all six individuals illustrated, more days were passed at the maintenance level than in any other single phase, although the periods spent in this manner were as variable as the other phases. In fact, a principal characteristic of the phases was their variability in occurrence and duration, both in the same individual and among members of the group.

Dominance Hierarchies.—Hierarchies among crustaceans under laboratory conditions have been reported for hermit crabs (Allee & Douglis, 1945), lobsters (Douglis, 1946) and crayfish (Bovbjerg, 1953, 1956; Lowe, 1956). In the crabbery, also, male *maracoani* arrange themselves daily in a dominance hierarchy, although this type of behavior is still too incompletely known to warrant comparison with the hierarchies in the previously-mentioned crustaceans. The following characteristics were, however, plainly evident throughout the period of observation.

Individual *maracoani* in the display phase are dominant to other individuals. Active crabs in the categories showing no aggressive behavior (Phases 2 and 3) always give way to all individuals in the higher categories; no agonistic behavior whatever is shown when individuals in these two categories meet. Among displaying individuals size often but not always determines dominance, and only straight-line hierarchies have been observed. Finally, a long-dominant or very large individual that has recently subsided into a maintenance phase may still dominate an aggressor in the aggressive wandering phase or even, rarely, a crab in the display phase.

A low-tide observation period of about two hours proved to be more than sufficient to determine the phase for that day of every male in the group, and to arrange them in the hierarchy applicable for the day. The same hierarchy never held for more than several days in succession. During the more inactive portions of the semilunar periods social activity was at such a low level that the hierarchy system was scarcely discernible.

Because of the importance of wandering individuals in the hierarchy, it seems that dominance relationships between individuals can rarely be established in the field to the extent they are noticeable in the crabbery; here the wanderers are forced repeatedly to encounter the same individuals.

Territoriality.—Altevogt (1957) reported that territoriality in the restricted sense of defending or remaining attached to a single burrow for a prolonged time does not exist in the species he was studying (*annulipes* and *marionis*). My own observations agree with his, particularly in the case of *marionis*. In this species, as in many primitive and semi-primitive species, waving takes place whether or not a burrow is, at the moment, being held.

In highly evolved species territoriality is much better developed. In *maracoani*, as in a number of other advanced species in different branches of the genus, a particular burrow may be defended by the same individual throughout a single display phase, often lasting a number of days. In these species no waving takes place before the crab has taken over a burrow either through its own aggression or through default by a previous tenant; this burrow is then defended from approaching aggressors, either by threat postures or by physical combat (p. 125 ff.) No waving occurs except within a few inches of the burrow, and in some small species the mouth of the burrow itself appears to comprise the entire territory, the crab normally threatening and displaying only when one or more tarsi are actually touching the rim of the hole. Even when a display-phase crab has defended a given burrow for several days, it does not wave during its infrequent periods away from the territory. Unless pursuing a female or briefly attacking a neighboring male slightly lower in the hierarchy, these absences usually consist, in *maracoani*, of direct trips through the population to the water's edge to feed; they are followed by returns, equally direct, to the burrow.

It is of course true that fiddlers in the non-aggressive phases (1-3 in *maracoani*) all occupy burrows at least during high tide, and that fiddlers of almost all species typically feed in the vicinity of the burrows, down which they descend when alarmed or at the approach of the tide. These burrows are, however, never defended against aggressors and there seems, at present, to be no definable bond between such a crab and a particular burrow. In these cases there appears to be no question of territorial behavior in the usual zoological senses of the word.

Many burrows, however, are held and defended for very short periods by crabs which, although physiologically in one of the upper phases (5 and 6 in *maracoani*), are yet rather low in the day's hierarchy and so easily dispossessed. Yet, during these periods of occupancy the tenant often shows territorial behavior as emphatically as do long-established tenants. It thus remains difficult and probably unrewarding to place a lower limit on the time a burrow shall be defended in order to qualify the occupant as a territory-holder.

The widely varying degrees to which territoriality is developed in *Uca*, and its fluctuations within individuals as described in the preceding pages, make its comparative study within this group of special biological and evolutionary interest. Until the completion of this aspect of the work, Thorpe's definition of territory as "any defended area" will remain particularly useful.

Activity Phases in Relation to External Conditions.—Under adverse external conditions individual response is related to activity phase. As conditions deteriorate, socially inactive crabs are the first to be affected. Vice versa, crabs in full display condition are exceedingly tolerant of poor environmental conditions of various kinds. Such low-threshold individuals often display in spite of dull weather, high temperature, imminent tides or adverse days of the semilunar period. In any field population numerous crabs are of course simultaneously in this low-threshold condition. Their conspicuousness is misleading, and makes casual observations on activity levels in relation to external conditions of little value.

A preliminary series of dissections shows that there is a gradual development and decline of the reproductory organs over a period of months, so that the short behavior cycles cannot be attributed directly to the seasonal development of gonads, nor is evidence available that the production of a spermatophore is involved. Almost certainly, however, the phases will prove to be hormonally controlled, whether through the activity of the sinus or other glands or through neural hormones. A phenomenon possibly related to the wandering phase of *Uca* was reported by Bliss (1953), when she observed that eyestalkless land crabs (*Gecarcinus*) were hyperactive.

Seasonal rhythms were apparent in various parts of the ranges in some of the common, widespread species of *Uca*: *marionis* in Fiji, Australia, Singapore, Zanzibar and Mozambique; *annulipes* in Singapore, Ceylon and Africa; *inversa* in Eritrea, Zanzibar and Mozambique, and a number of species, particularly *rapax*, in the neotropics. All of these show evidence that populations near the beginning of the breeding season include on any day more individuals in the aggressive wandering phase, and that more fighting takes place, than later in the season, when waving is at its peak.

V. Postures and Motions Associated with Social Behavior in *Uca maracoani*

Through the work in the crabbery, a special study was made of the postures connected with social behavior in *U. maracoani*, a species which is highly developed socially. Many of the postures and motions have been observed in most or all of the other species studied in the genus in either identical form (as in high-intensity fighting) or with slight variations; others appear to be more restricted.

In any case, Text-figures 2-5 inclusive, in association with the explanations below, should serve as a useful standard and comparison for equivalent behavior in other species of the genus.

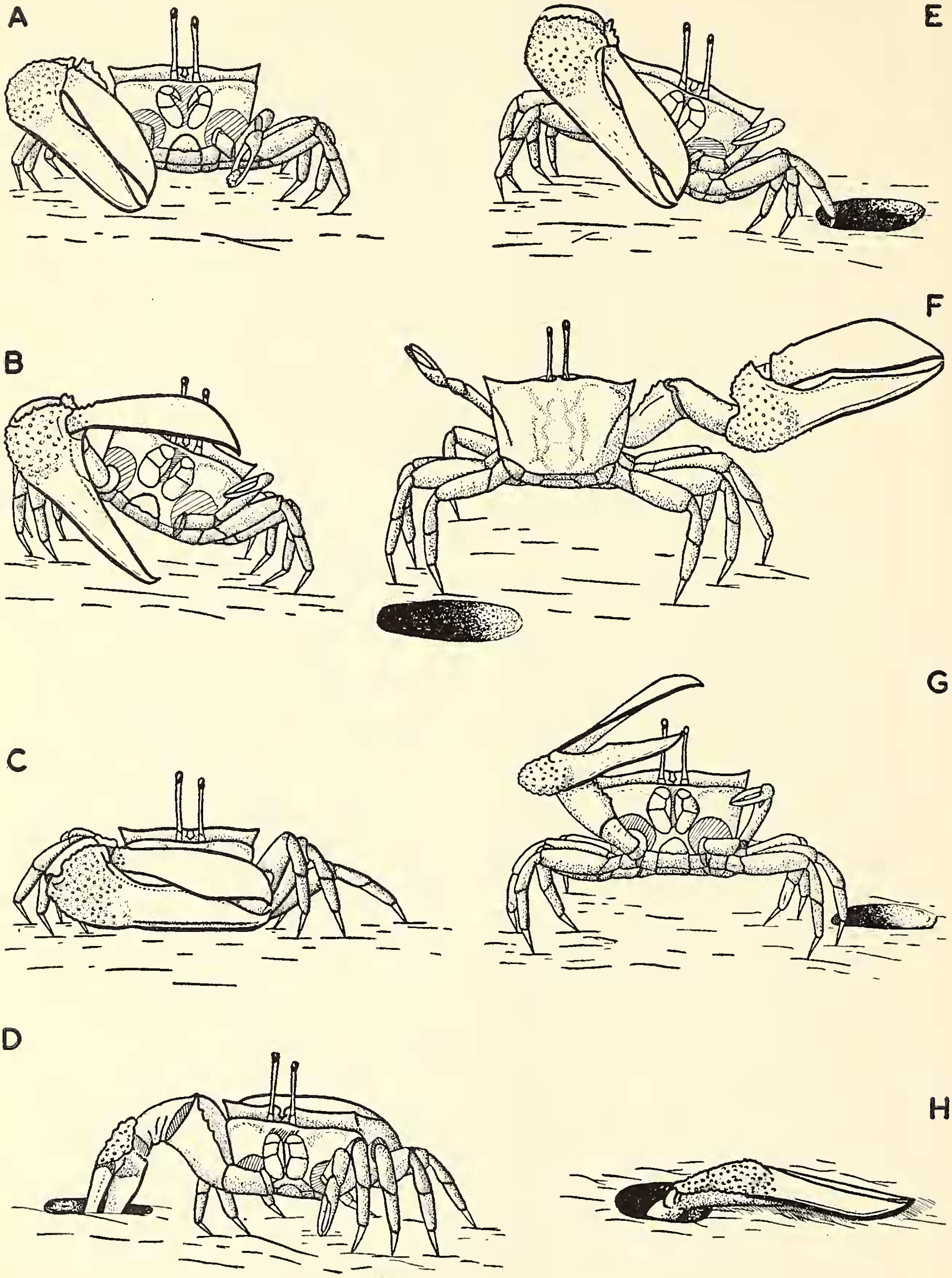
Text-figure 2. *Agonistic Behavior in Uca maracoani.* In A-D inclusive the activities illustrated are not necessarily associated with the tenancy of a burrow. In E-H inclusive the individual always shows attachment, however temporary, to a particular hole.

A. *Threat*: *Lowest Intensity*. *Posture*: Body scarcely or not at all elevated; base of major manus slightly raised, not over-reaching height of erect eye. Chelae closed, the tips touching ground or nearly so. *Motion*: Cheliped moved back and forth, forward and slightly sideways, in narrow arc; true feeding usually continued. *Occurrence*: This behavior may occur in males in the three upper phases, when feeding at a distance from a burrow, usually at the water's edge; it occurs when the feeding crab is crowded or approached by another individual, male or female.

B. *Threat*: *Medium to High Intensity*. *Posture*: Major side of body and base of major manus moderately elevated; pollex pointed obliquely down, chelae widely opened. *Motion*: Walking present or absent. *Occurrence*: Assumed by males in either aggressive wandering or display phases, in either aggression or defense. An aggressive wanderer may employ it in approaching any burrow held, however temporarily, by a male in any phase, that is standing close to it. It is also often used by a burrow's tenant, in a display or predisplay territorial phase, at the approach of another male. By whichever crab it is inaugurated, it often elicits the same posture in the opponent. Pressure of the apposed open chelae follows more rarely (as in Text-fig. 3A or 3B) and linked chelipeds (3C) most rarely of all.

C. *Submissive-escape Behavior*. *Posture*: Body and major cheliped barely clear ground. *Motion*: Walking, usually with the major cheliped leading. *Occurrence*: Characteristic of males in the maintenance or wandering phases, or of a display phase male which has been displaced from his burrow by threat or by prying out, by another individual higher in the dominance hierarchy. Finally, it is sometimes assumed by the retreating loser following an actual fight (Text-fig. 3).

D. *Exploratory Behavior*. *Posture*: Major cheliped inserted in burrow, body partially elevated. *Motion*: Slight thrusting movements of chelae. *Occurrence*: May be performed by any male about to enter a strange burrow or its own burrow after an absence, apparently when there is at least a possibility of its occupancy by another crab, male or female. Also performed as a preliminary motion to pry out another crab, male or female, as when a dominated individual such as illustrated in C, having been pursued, has escaped down a burrow. Actual entering of a burrow and prying out are almost always



TEXT-FIG. 2. A-H, Agonistic behavior in *Uca maracoani*. For explanation, see text, p. 123 ff. Drawings by Julie C. Emsley.

accomplished by the ambulatories of the opposite (minor) side, the crab first withdrawing the large cheliped and turning completely around.

E. *Burrow Defense*: *Low Intensity*. *Posture*: Similar to A, the non-territorial equivalent, but base of major manus and entire major side are well elevated. Often the minor ambulatories are half concealed in burrow. *Motion*: None, except to face potential opponent. *Occurrence*: Assumed only by display-phase males when adjacent to their currently occupied burrows. The stimulus is the approach or near passing of another male in any phase.

F. *Burrow Defense*: *Medium Intensity*. *Posture*: Body elevated, chelipeds outspread horizontally. *Motion*: None, except to present vertically tilted carapace to potential opponent. *Occurrence*: Usually follows preceding posture, E, as the stimulating crab passes to the side and/or rear of the burrow's tenant. In that case, E shifts smoothly into F. Alternatively, F is assumed when a potential aggressor approaches from the rear. As in E, only a male in the territorial or display phase assumes this posture.

G. *Burrow Defense*: *High Intensity*. *Posture and Movement*: This is true display, typical of the species, with the cheliped making a somewhat circular "wave" and not returning to the ground between displays. Body and cheliped both moderately elevated, the tips of the chelae reaching their maximum somewhat above eye level. There is no walking during display, although the crab may turn to remain facing the stimulus. The high elevation of the body contrasts with its low level in the submissive individual shown in C. Although the display represents the highest intensity of burrow defense behavior short of fighting, it is low intensity as far as display is concerned. The cheliped is rotated slowly, with an outward, up and down movement typical of lateral displays except that the cheliped is not brought to the ground between waves. In contrast to high-intensity courtship (Text-fig. 5B, C) the tempo is slow, the circular "windmilling" of the chelae is not accented, both the stretch of the ambulatories and the reach of the cheliped are moderate, the carapace is not tilted so far back as to be vertical and the crab always faces its opponent, if any. *Occurrence*: Found, by definition, only in display phase males, and then only when they are within a short distance of their burrows, usually several inches or less.

The display described above often occurs within an apparent vacuum—that is, without apparent stimulus from another individual, even of another species. This is best seen during adverse tides or weather in the crabbery, when occasionally only a single individual—a *maracoani* in full display phase—is on the surface. Such individuals customarily erupt rapidly from their burrows and commence display at once. The vacuum character of such displays is understandably nearly impossible to establish under field conditions, because the excellent eyesight of the crabs makes the range extent of possible stimuli difficult to determine. Display also is frequently initiated at the approach of males and apparently by distant or motionless females. Often it precedes or follows E or F, or the sequence E, F, or, with equal frequency, B, when the crab is a burrow tenant.

H. *Burrow Defense and/or Individual Defense, Lowest Intensity*. *Posture*: Only the cheliped, the chelae usually completely closed, is left flat outside the burrow. *Motion*: None. *Occurrence*: This behavior is characteristic of crabs in the beginning of a territorial phase, when approached by an aggressively wandering male, particularly one in B posture. It also occurs in display phase males when approached by an aggressive wandering or display phase male higher in the hierarchy. Under the latter conditions this behavior is sometimes even preceded by low intensity display as in G.

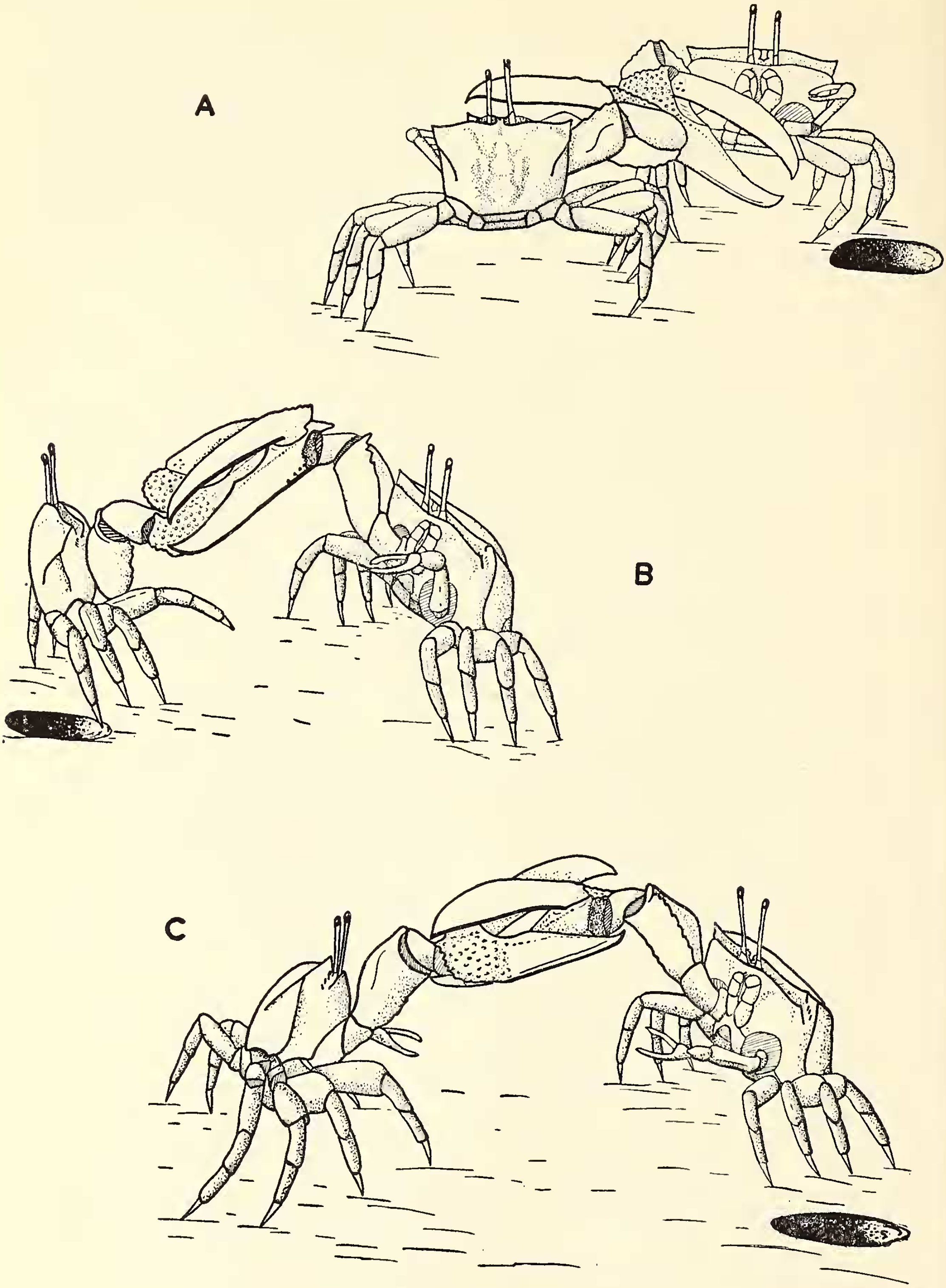
Text-figure 3. *Fighting in U. maracoani*. Fighting, as opposed to mere threat, is here defined as any behavior between two males in which the major chelipeds are brought into contact. No fights occur in this species unless one of the crabs is close to a burrow of which he is the tenant. All of the types of fighting are much rarer than any of the threat gestures previously described, and only crabs in the aggressive wandering, territorial or display phases are involved.

Altevogt's illustrations (1957, pp. 64-65) of one threat gesture and two kinds of fighting in *marionis* clearly show corresponding postures in another species.

A. *Low Intensity*: *Manus-to-manus Pushing*. The direction is back-and-forth. Maximum result: One crab is forced backward, and retreats, often in a hasty skid.

B. *Medium Intensity*: *Manus-to-pollex Pushing*. The curved, externally concave end of the pollex fits under the heel-like, tuberculous surface of the lower base of its opponent's manus, giving good leverage. Obviously this position is impracticable when opponents have claws of opposite sides enlarged. A complete upsetting by this means has not been observed, although one of the crabs is often thrust off balance and rapidly retreats.

C. *High Intensity*: *Chelipeds Interlocked*. Of relatively rare occurrence. Crabs push back and



TEXT-FIG. 3. A-C, Fighting in *Uca maracoani*. For explanation, see text, p. 125 ff. Drawings by Julie C. Emsley.

forth and pry upward. The ultimate, exceedingly rare climax is the complete overturn of one of the crabs. No physical damage of any kind has ever been observed in any of these types of fighting.

Text-figure 4. *Courtship Away from Burrow of Male.*

A. *Rejection Posture of Female*: At the approach of a male, an unwilling female partially descends her burrow, leaving the legs of one side projecting stiffly above the ground. Successful efforts to pry out and court such a female have not been observed.

B. *Ritualized Feeding.* The male climbs on top of a female and makes plucking motions at frontal, suborbital and especially the tuberculous antero-lateral regions of her carapace. The male's minor chelae are brought to his buccal region as in feeding, but actual feeding, from the scanty mud clinging to the female, does not take place; often the cheliped is not brought all the way to the mouth and no pellet (dropped or wiped away in true feeding) is ever formed at the base of the maxillipeds. In addition to the ritual feeding the male's ambulatories sometimes stroke the female's carapace and legs, in addition to the male's obvious ultimate motions involved in turning her over into the position shown in C. At the beginning of ritualized feeding the female may be struggling, her body held high on rigidly braced legs. She gradually relaxes into the quiescent position shown in B.

C. *Copulation at Surface.* The position of the major cheliped varied in the half-dozen surface copulations seen in this species, but it played no particular part in holding the female and the chelae only once touched her at all.

Text-figure 5. *Courtship Display at Mouth of Male's Burrow.*

A. *Routine Low Intensity Display* (as in Text-fig. 1G). This behavior occurs by the hour in males at the peak of the display phase. When directed toward an individual, whether male or non-approaching female, the crab always faces in that direction.

B. and C. *High Intensity Courtship Display.* Elicited only by an approaching female. Compared with A, the carapace is held higher and tilted vertically back, the cheliped reaches higher and rotates faster in a much wider arc, the chelae are widely opened and one or two ambulatories, first on one side and then on the other, are elevated, in accordance with the momentarily shifting balance of the great claw. During the high intensity display the crab always presents the carapace toward the approaching female, who generally does not approach steadily but in spurts interrupted by pauses. These pauses do not interrupt the male's display. The female after such an approach usually bypasses the male, in which case the quality of his display subsides to low intensity (as in A) or ceases altogether almost at once. Occasionally, however, a female approaches almost beneath him (C) whereupon he swiftly descends the burrow (minor side first, as usual). The female then either passes on or follows the male at once. In the latter case she may or may not stay below, presumably copulating.

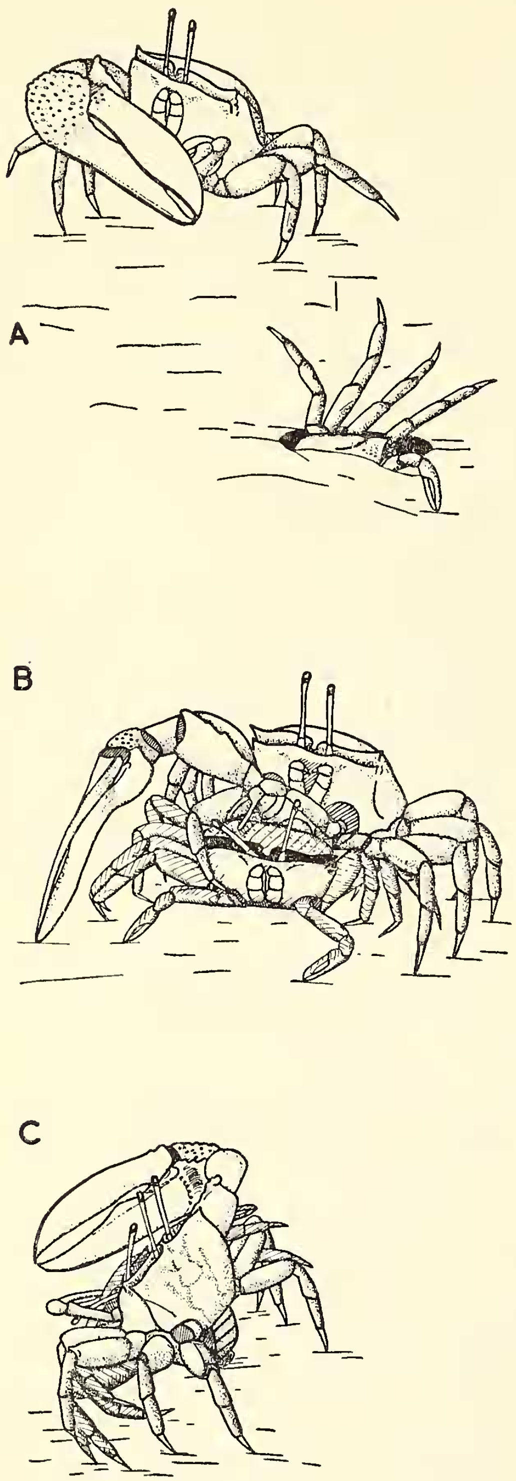
In *maracoani* the behavior illustrated in Text-figure 4 seems to be characteristic of pairs where the female is less ready to mate than the male. It is the only type of mating found in the primitive species of the genus (Crane, 1957). Also, 4B often occurs where the male is not in full display phase; in these latter instances copulation has never been observed to follow.

The behavior illustrated in Text-figure 5, on the other hand, is in this advanced species the more typical. There is evidence that it is females which have recently molted, although hardened, that are in the wandering phase that stimulates high intensity waving. It also seems likely that odor plays a minor role, since at least in this species not all moving females stimulate strong waving from males. Nevertheless in many other advanced forms a male without major cheliped, or a dried female on a string, is enough to release high intensity waving (Burkenroad, 1947; Altevogt, 1957; Crane, unpub.).

VI. Summary

In order to supplement field observations on comparative social behavior in the genus *Uca*, four species were maintained in an out-of-doors terrarium in Trinidad. Throughout a period of four months detailed records were kept of the daily activities of individual *U. maracoani*, while additional data were assembled on *cumulanta*, *rapax* and *thayeri*.

All the species showed strong tidal and semilunar rhythms in their social activities, similar to those known partially to control the expansion of chromatophores in northern species. The successful use of the terrarium depended on an arrangement of tides and observation schedules roughly in accordance with these rhythms. No attempt was made either to determine their periods with laboratory precision or to alter them experimentally. The semilunar rhythms apparently depended on a favorable juxtaposition of time of day with local hours of low tide. Differences among the species were evident in the timing of the optimum period of social activity each fortnight.



TEXT-FIG. 4. A-C, Courtship in *Uca maracoani.* For explanation, see text, p. 127. Drawings by Julie C. Emsley.

Apart from behaving in accordance with the above rhythms, each individual adult male showed cycles of social behavior that culminated in a display phase. In *maracoani* the preceding stages lead from a period of inactivity underground, through a simple maintenance routine (feeding and digging), a wandering phase, one of aggressive wandering and a phase in which a burrow was defended as a territory. The subsequent display phase, which sometimes persisted for a number of days and occurred several times a season, occasionally culminated in full courtship and, rarely, in mating. The phases were highly variable in duration both within single individuals and among members of the group, and in any cycle one or more phases were often superimposed or omitted.

A special study was made of social postures and motions in *maracoani.* The males showed an extensive repertory, the various components being elicited in response to specific situations of an agonistic or epigamic character. Most of the postures have their equivalent in other species of the genus; some are characteristic only of species in which territoriality is more or less developed; a few, including one fighting pattern and display itself, are specifically distinct.

Under terrarium conditions a distinct dominance hierarchy was found to occur in *maracoani.* The order was never maintained for more than several days at a time, apparently because of the changing phases of the individuals. Crabs at the top of the day's hierarchy were almost always in the full display phase. Rarely an individual just past a long-maintained display phase was still dominant to one or more displaying males which he had previously dominated. The hierarchy showed in encounters even when both males were in the display phase, the same crab being dominant at least during a single low-tide period. Between such individuals which were well matched in phase, comparative size was usually but not always a factor of importance. Between two individuals well separated in the hierarchy the lower individual always retreated without fighting, and usually in a low-crouching position. Because of the prevalence of wandering phases it seems probable that most hierarchies in the field are even more temporary than in the terrarium.

The governing influences and specific variety of characteristics controlling social behavior in the crabbery are certainly prevalent throughout the genus. Before the start of the Trinidad work, field studies on many species in both hemispheres had already given preliminary evidence of the existence of tidal and semilunar rhythms, the occurrence of phases in individuals and the wide variety of postures and motions characteristic of highly evolved species. The prolonged observations of individuals in captivity provided an invaluable supplement to basic studies of wild populations.

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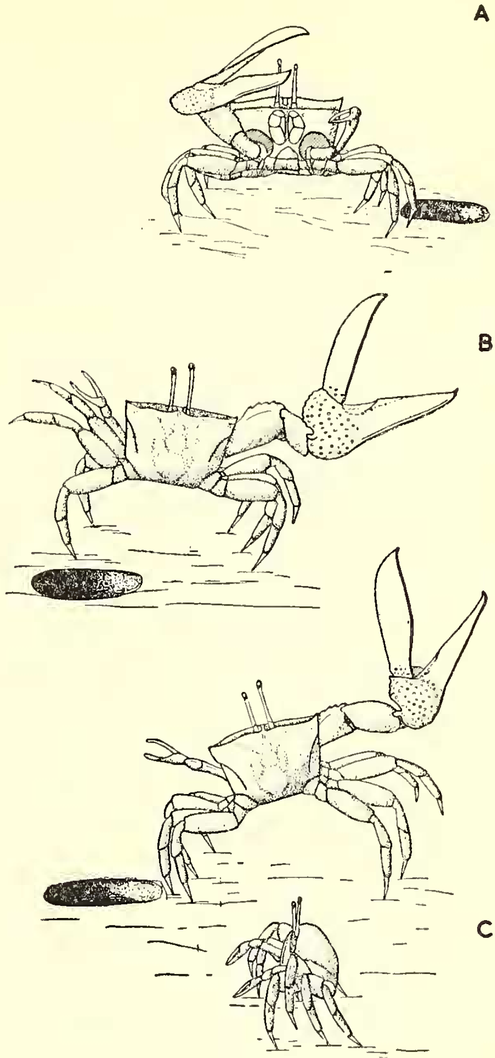

Text-fig. 5. **A-C,** Courtship in *Uca maracoani*. For explanation, see text, p. 127. Drawings by Julie C. Emsley.

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EXPLANATION OF THE PLATE

PLATE I

Outdoor terrarium for fiddler crabs, showing mud-bank with burrow markers, fence of wire netting to keep out toads, and hose for raising water level to simulate a rising tide. See text, p. 114 ff.